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FURTHER STUDIES OF MORPHOLOGICAL DIFFERENTIATION IN SPOTTED AND SPINNER DOLPHINS (*Stenella attenuata* AND *S. longirostris*) FROM THE EASTERN TROPICAL PACIFIC

By

Gary D. Schnell, Michael E.
Douglas and Daniel J. Hough

ADMINISTRATIVE REPORT LJ-85-04C

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by

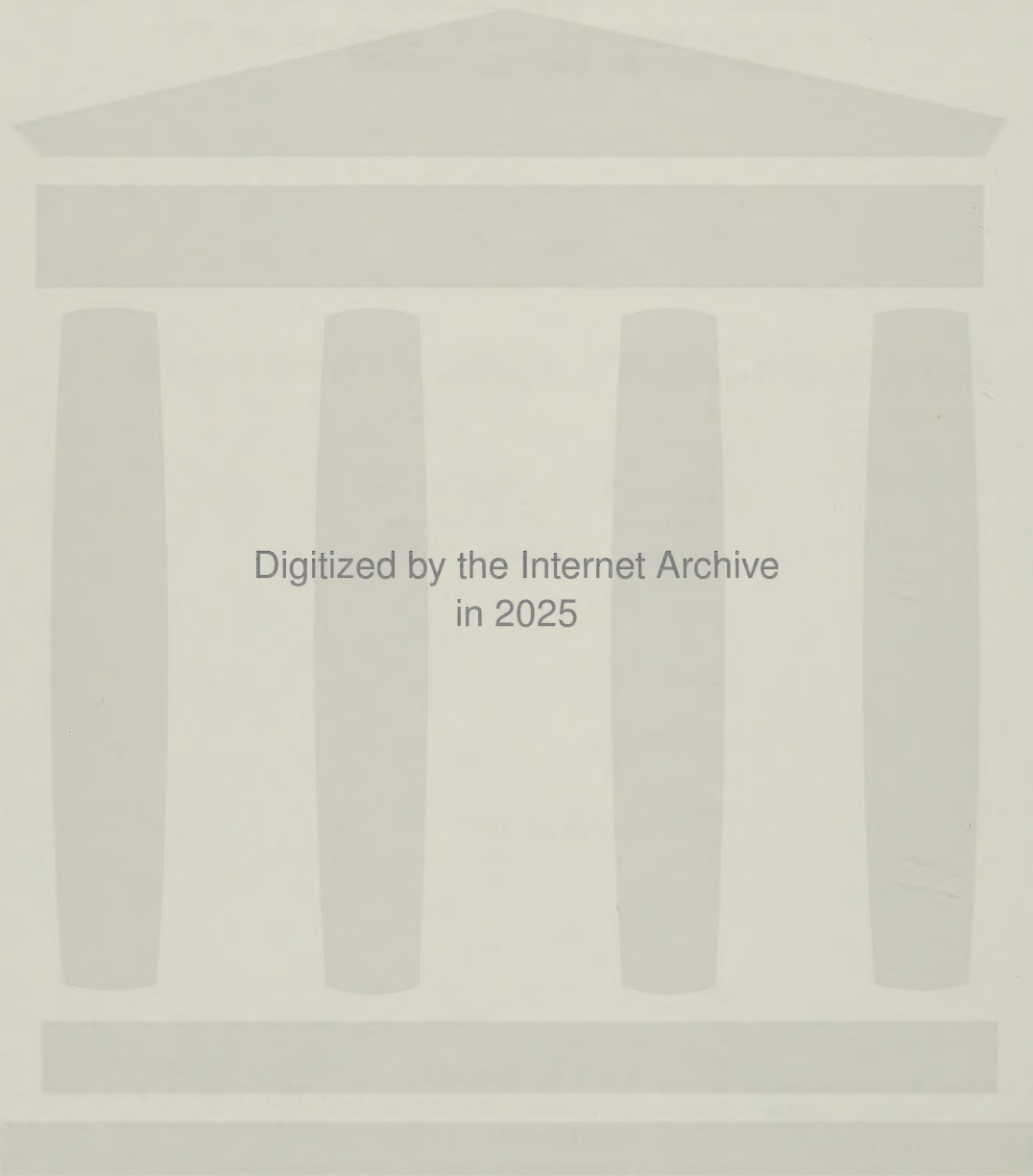
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TABLE OF CONTENTS

ABSTRACT.....	ii
INTRODUCTION.....	1
MATERIALS AND METHODS.....	1
<u>Northern-Southern Spotted Dolphin Differentiation</u>	1
<u>Northern-Southern Spinner Dolphin Differentiation</u>	2
<u>Whitebelly-Eastern Spinner Dolphin Differentiation</u>	2
<u>Northern-Southern Whitebelly Spinner Dolphin Differentiation</u>	4
<u>Eastern, Northern Whitebelly, and Southern Whitebelly Spinners</u>	4
RESULTS.....	4
<u>Northern-Southern Spotted Dolphin Differentiation</u>	4
<u>Northern-Southern Spinner Dolphin Differentiation</u>	5
<u>Whitebelly-Eastern Spinner Dolphin Differentiation</u>	5
<u>Northern-Southern Whitebelly Spinner Dolphin Differentiation</u>	7
<u>Eastern, Northern Whitebelly, and Southern Whitebelly Spinners</u>	7
DISCUSSION.....	7
<u>Northern-Southern Spotted Dolphin Differentiation</u>	8
<u>Northern-Southern Spinner Dolphin Differentiation</u>	9
<u>Whitebelly-Eastern Spinner Dolphin Differentiation</u>	9
<u>Northern-Southern Whitebelly Spinner Dolphin Differentiation</u>	9
<u>Eastern, Northern Whitebelly, and Southern Whitebelly Spinners</u>	10
ACKNOWLEDGMENTS.....	10
LITERATURE CITED.....	10
TABLES.....	12
FIGURES.....	19

ABSTRACT

In an earlier study (Schnell et al. 1982), extensive analyses were conducted of geographic variation in cranial morphology (36 measures) of spotted and spinner dolphins (Stenella attenuata and S. longirostris) in the eastern tropical Pacific. These analyses were extended to determine the degree of differentiation between northern and southern populations of spotted dolphins, as well as between such populations for spinner dolphins. Also, cranial differences between whitebelly and eastern spinners were assessed.

Using a discriminant function involving 10 skull characteristics, over 87% of available spotted dolphin specimens could be correctly identified as to whether they were from the north or south. A pseudo-jackknifed procedure was used that "corrects" for the fact that the specimens being evaluated were those initially used to construct the function. The differences in northern and southern spotted dolphins are notable and support recognition of the southern spotted dolphin as representing a largely separate population from those found to the north.

If all spinner dolphin specimens are used (irrespective of color type), the northern-southern distinction in spinner dolphins is even more pronounced; over 94% of the individual animals were correctly allocated to geographic area on the basis of seven skull measurements. Separate recognition of northern and southern entities is supported by this analysis.

For whitebelly and eastern spinner dolphins, we found no substantive differences in the degree or extent of sexual dimorphism in skull characteristics. Thus, corrections that have been used to partition out the effects of sexual differences on variation in spinner dolphins were judged to be applicable to both color forms in the eastern tropical Pacific.

Separation of whitebelly and eastern spinner dolphins is possible using a function developed for cranial characters, with 92% of the specimens being correctly identified. If one analyses only specimens from areas where the two color forms are sympatric, about 83% could be correctly identified.

Restricting the analysis to northern and southern whitebelly spinners, it was possible to correctly allocate approximately 84% of these animals to their group. When three groups were assessed--eastern, northern whitebelly, and southern whitebelly spinners--it was still possible to identify over 82% of the specimens correctly.

Overall, cranial morphometric differences are present between whitebelly and eastern spinners, with even stronger differentiation between northern and southern spinners. The morphological data for this species, as well as for the spotted dolphin, clearly indicate that populations are geographically subdivided in the eastern tropical Pacific in such a way that gene flow is restricted.

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INTRODUCTION

Schnell et al. (1982) conducted a detailed analysis of geographic variation of spotted and spinner dolphins (Stenella attenuata and S. longirostris) in the eastern tropical Pacific Ocean. They studied morphometric variation in skulls, as well as body length variation. Subsequently, some aspects of their analyses have been published elsewhere (Douglas et al. 1984, Schnell et al. 1985). As a result of their investigation and subsequent detailed review of their findings, it became clear that further study of the available data could extend and expand understanding of differentiation within these two dolphin species.

In this report, using cranial dimensions, we provide additional analyses of: (1) differentiation between northern and southern populations of spotted dolphins; (2) differentiation between northern and southern populations of spinner dolphins; (3) spinner dolphin variation, taking into account the designation of specimens with respect to whether they were "whitebelly" or "eastern" spinners based on external morphological criteria (Perrin 1972, 1975a, 1975b); (4) differentiation between northern and southern whitebelly spinner dolphins; and (5) differentiation among eastern, northern whitebelly, and southern whitebelly spinner dolphins.

MATERIALS AND METHODS

The skulls analyzed are the same as those available to Schnell et al. (1982). They indicated the number of specimens from each 5° latitude-longitude block in figures 2 and 3 (Schnell et al. 1982), respectively, for spotted and spinner dolphins. We used the same 36 meristic and morphometric skull characters (table 1 and fig. 5 of Schnell et al. 1982). Typically, we used "zwitter" measurements, where values were corrected appropriately to allow for the combining of specimens of the two sexes for individual analyses (see explanation in Schnell et al. 1982, 1985).

Northern-southern spotted dolphin differentiation.—Schnell et al. (1982) and Douglas et al. (1984) confirmed the distinctness between inshore and offshore spotted dolphins. In addition, Schnell et al. (1982) demonstrated a strong subdivision between northern and southern populations (a difference first noted by Perrin et al. 1979), with the sample from the most westerly location also being somewhat different from those in the north and south.

In order to further assess differentiation between northern and southern populations, we considered only offshore spotted dolphins and

eliminated the seven specimens from the far western locality (block 0501 in fig. 2 of Schnell et al. 1982; see Fig. 1) for this particular analysis. As a result, 567 specimens were used—503 from the northern area and 64 from the southern area. The number of specimens from each block included in the analysis is shown in Figure 1.

A stepwise discriminant analysis (Program P7M of BMDP-83; Dixon 1983) was used to find the linear combination of variables which best characterizes differences between the northern and southern areas, given the within-group variances of individual characters. The F -value to enter was set at 4.0; thus, a character was added to the function only if this degree of additional separation between the two groups was obtained. Projections onto the discriminant and classification functions were derived to assign specimens to one of the two groups, depending on the relative probability of group membership. Coefficients for the discriminant function are presented as both unstandardized and standardized (i.e., by pooled within-group variances) values. The unstandardized coefficients can be used with actual measurements (corrected to zwitter values) to project specimens onto the discriminant function; standardized coefficients can be used with measures expressed in standard deviation units from the mean.

The classification functions are based on an equal probability of a particular specimen being from the north or the south. Measurement values for the specimen are multiplied by the coefficients of the classification function, and the resulting products are added to the constants of the functions. The calculation is completed for both classification functions, and a specimen is assigned to the northern or southern group, depending on which of the resulting classification values is the greatest.

We also used a pseudo-jackknifed classification procedure (see Dixon 1983), which effectively leaves out the individual specimen being considered, recomputes the coefficients of the functions, and then evaluates the specimen; typically, this procedure gives a better indication of the future behavior of functions on new specimens (i.e., those not used to compute the functions).

Northern-southern spinner dolphin differentiation.—A similar analysis was performed to assess the degree of north-south distinctness in spinner dolphins, which we (Schnell et al. 1982) found earlier and was originally suggested by Perrin et al. (1979). Since the coastal or Costa Rican form was found to be very different from other spinner dolphins (Schnell et al. 1982; Perrin 1975b), we did not consider it in this analysis. In addition, a few specimens were eliminated from the samples because they had not been identified as having been whitebelly or eastern spinners (based on external criteria and of interest in further analyses). The remaining 193 specimens were studied—138 from the north, 53 from the south, and 2 treated as "unknowns" (see Fig. 2).

Whitebelly-eastern spinner dolphin differentiation.—Perrin (1972, 1975a, 1975b) described two color patterns in spinner dolphins of the eastern tropical Pacific Ocean—an eastern form to the north and northeast, and a whitebelly form to the south and and southwest. In our initial report (Schnell et al. 1982), we did not take into account this

difference in specimens, since both are considered part of the same species and there is some overlap in their distributions.

However, given that 193 of the 196 specimens (not counting the four Costa Rican specimens) summarized in our earlier report (Schnell et al. 1982:fig 3) were known from collection data to be whitebelly or eastern, it is possible to assess morphometric skull differences of the two types. A map showing the geographic distribution of the 103 eastern and 90 whitebelly spinners is included as Figure 3.

The first analysis involved the evaluation of our zwitter correction of sexual differences, since we had developed the correction on the basis of spinner specimens, irrespective of color pattern. Therefore, we conducted a two-way analysis of variance (ANOVA) for each of the 36 characters using SAS (SAS Institute Inc. 1982) with the factors being sex and color. This ANOVA was used on specimens from the single block with the largest number of specimens (0504; see Fig. 3) in order to eliminate differences that might be due to geographic variation. Of the 8 eastern spinners from this block, 2 were males and 6 were females, while of the 17 whitebelly spinners, 9 were males and 8 were females.

Since the number of specimens from block 0504 is relatively small, albeit the largest from any given block, we also conducted a similar analysis combining specimens from blocks where the eastern and whitebelly spinners are likely in sympatry--0501, 0504, 0505, 0506, 0507, and 0409 (see Fig. 3; although we had specimens of only one form from 0507 and 0508, both color types probably occur in these blocks). This combined sample of 59 specimens included 8 male and 18 female easterns, and 18 male and 15 female whitebellys. This analysis is more likely to confound geographic factors with those of color and sex but, at the same time, the samples are larger.

If a significant interaction was found for a character between sex and color in these two analysis, it would indicate that sexual dimorphism was different in the two color types; lack of significant statistical interaction would suggest that our initial treatment of sexual dimorphism by using the same correction in both color forms was appropriate. Since there was little evidence of interaction of the sex and color factors (presented in Results), subsequent analyses were conducted using zwitter values and the sexes combined.

In order to evaluate overall variation of eastern and whitebelly spinners, the 193 specimens were subjected to principal components analysis (Sneath and Sokal 1973) using NT-SYS (Rohlf et al. 1982). Characters were standardized, so that the means were zeros and standard deviations one. Specimens were projected onto the first two principal components extracted from a matrix of correlations among the standardized characters. Also, a stepwise discriminant analysis (as described earlier) was conducted to determine the degree of separation possible between eastern and whitebelly spinner forms based on skull measures.

Since the eastern and whitebelly spinners have broad portions of their respective ranges that are allopatric and, thus, differences could

simply reflect geographic variation, we conducted a series of analyses restricted to the 59 specimens from those blocks where the two color forms are likely to overlap in distribution: 0501, 0503, 0504, 0505, 0506, 0507, 0508, and 0409 (see Fig. 3). This more limited sample is not strongly influenced by the marked north-south geographic trend in variation present in spinner dolphins (Schnell et al. 1982), since all blocks but one are between 5° and 10° north latitude (and the other spans from 0° to 5° N).

A principal components analysis (see above) was completed, and the 59 specimens were projected onto the resulting components. Also, using the standardized data for the 59 specimens, we calculated average distance coefficients for all pairs and applied the unweighted pair-group method using arithmetic averages (UPGMA) as a clustering technique (Sneath and Sokal 1973; NT-SYS). The cophenetic correlation coefficient was computed to indicate the degree to which distances in the resulting dendrogram represented the original multivariate distances between specimens. Neither the principal component analysis nor the cluster analysis require a priori assignment of specimens to groups and, thus, provide an indication based on multiple cranial characters of the degree of difference between the two color types. We also completed a stepwise discriminant analysis (as described above) on the 59 specimens to determine the degree of separation that can be achieved between the two forms in this more limited geographic range of overlap.

Northern-Southern Whitebelly Spinner Dolphin Differentiation.--We also evaluated the degree of north-south differentiation in spinner dolphins if only whitebelly spinners are considered (i.e., deleting eastern spinners from the analysis). The analyses performed were the same as those employed to assess north-south differences for the total sample of spinner dolphins. A total of 90 specimens were studied, including 35 from the north, 53 from the south, and 2 treated as "unknowns."

Eastern, Northern Whitebelly, and Southern Whitebelly Spinners.--A final analysis was completed that considered three groups simultaneously--eastern, northern whitebelly, and southern whitebelly spinner dolphins. A stepwise discriminant analysis was used to find the combinations of variables which best characterized differences among these three groups. Projections of individual specimens were obtained on the resulting canonical variables, and classification functions were developed to assign specimens to one of the three groups. As in other classification functions, groups were assigned equal probability of membership. The total of 193 spinner dolphins were assessed: 103 eastern; 35 northern whitebelly; 53 southern whitebelly; and 2 unknown.

RESULTS

Northern-southern spotted dolphin differentiation.--For the discriminant analysis, a total of 10 characters were selected to achieve separation of the spotted dolphins from the two geographic areas (Table 1). The best single character for separating northern and southern spotted dolphins was Preorbital W. (see from Table 1 that it was the initial variable entered into the discriminant function) although, when

taken in combination with and adjusted for the other nine characters, the F-value to enter for W. Temporal Fossa is actually higher.

A plot of all specimens projected onto the discriminant function is depicted in Figure 4. Although overlap exists, the 10 discriminating characters provide considerable separation between northern and southern spotted dolphins. The bar graph also shows the position of the seven specimens from block 0501; they were not included in the groups used to determine the discriminant function initially, but were projected onto the variable after character coefficients were determined. One of the seven is very much like typical northern specimens and four score like typical southern specimens; the other two are somewhat intermediate, with the classification functions indicating that they are closer to the southern specimens.

Of the 503 specimens from the northern area, 444 (88.3%) were identified correctly to area using the classification functions. For the 64 southern specimens, 56 (87.5%) were correctly identified. Overall, 88.2% of all specimens were appropriately allocated. Using the pseudo-jackknifed classification procedure (which should give a better indication of performance of classification functions on new specimens), the results were very similar. It identified 443 (88.1%) northern and 55 (85.9%) southern spotted dolphins correctly (87.8% of total).

Northern-southern spinner dolphin differentiation.--The discriminant function for differentiating between northern and southern spinner dolphins includes seven characters (Table 2). Clearly, Postorbital W. is the single most important character for separating the animals from the two areas. Figure 5 shows that almost complete separation of northern and southern spinners is achieved with the function.

Using the classification functions, 95.3% of the 193 specimens were correctly allocated with respect to region. They identified 131 (94.9%) of the 138 northern specimens, as well as 51 (96.2%) of the 53 southern animals. For the pseudo-jackknifed procedure, 94.1% were appropriately classified--128 (92.8%) of 138 northern spinners and 51 (96.2%) of 53 southern spinners. The two "unknowns" were identified as being more closely associated with members of the northern group.

Whitebelly-eastern spinner dolphin differentiation.--In the two-way ANOVAs for spinner dolphins from block 0504, only 2 of the 36 characters showed a significant interaction term ($P < 0.05$) between sex and color. These were W. External Nares and W. Internal Nares, both characters that did not show significant sexual dimorphism in earlier analyses (see table 18 of Schnell et al. 1982). Having 2 of 36 characters exhibit statistical significance is about what one would expect by chance alone.

Similarly, when the larger sample involving all blocks in the area of sympatry of whitebelly and eastern spinners, only 2 of the 36 cranial characters had significant interactions of color and sex--Skull W. (at Parietals) and Tooth W. Only the former is sexually dimorphic (table 18 of Schnell et al. 1982).

Figure 6 shows projections of the 193 spinner dolphins onto the first two principal components based on the 36 characters. We have indicated whether individual specimens were eastern or whitebelly in coloration. Schnell et al. (1982) conducted a component analysis of blocks of spinner dolphins, rather than individual specimens (see their fig. 21 and table 19). In the present analysis, the first component explained 41.9% of the total character variance, while the second accounted for 9.8% (total 51.7%). Not unexpectedly, this is somewhat less for the first component than found with the block analysis; additional individual variation is included in the current analysis.

The character associations with the two components in the present analysis are very similar (although somewhat less strong for the first component) to those reported by Schnell et al. (1982:table 19) and, thus, are not tabled here. The first component has relatively high correlations with most characters except for tooth counts. Animals to the right of Figure 6 tend to be larger in size, while those to the left are smaller. The second component has relatively high negative correlations with tooth characters; specimens toward the bottom of Figure 6 have slightly higher numbers of teeth and longer tooththrows. The whitebelly animals tend to be larger and are found to the right of Figure 6, although there is not a clear-cut separation of the two forms. There is no discernible difference between the two forms in terms of tooth characters and component II (Fig. 6).

Five characters were included in the discriminant function for separating eastern and whitebelly spinners based on the 193 specimens (Table 3). Postorbital W. is the most important single character, as it was for the northern-southern spinner analysis above. In Figure 6, the specimens are projected onto the discriminant function. The classification functions allocated 96 (93.2%) of the 103 eastern spinners correctly, as well as 83 (92.2%) of the 90 whitebelly spinners (92.7% correct for total sample). With the pseudo-jackknifed technique, 96 (93.2%) of the eastern and 82 (91.1%) of the whitebelly animals were assigned to the appropriate color group (92.2% of all specimens correct).

For the more limited sample of 59 eastern and whitebelly spinners from the area of sympatry, projections onto the resulting principal components are shown in Figure 8. Component I statistically explains 37.1% of the total character variance, while component II summarizes 11.4% (total 48.5%). Again, the first component is basically one of size, with smaller animals to the right in Figure 8, while the second reflects tooth characters, with higher tooth counts and longer tooth rows being found in specimens near the bottom of the plot.

The results of a cluster analysis of the same data is presented in Figure 9. Four of the specimens, representing outliers in Figure 8, are shown in the dendrogram (at the bottom) to be somewhat different from the other specimens. The remaining specimens are shown to be in two clusters, although they are not well defined. As indicated by the specimen labels in Figure 8, the clusters do not correspond to any eastern-whitebelly subdivision--both color types are included in the two clusters.

The results of a discriminant analysis using the 59 specimens are shown in Table 4 and Figure 10. The four characters listed in Table 4 provide for separation of eastern and whitebelly spinners (Fig. 10), although there is overlap. Classification functions were able to correctly identify 22 (84.6%) of the 26 eastern spinners and 28 (84.8%) of the 32 whitebelly spinners (84.7% of total correctly allocated). With the jackknifed procedure, 21 (80.8%) of the eastern and 28 (84.8%) of the whitebelly specimens were appropriately classified (83.1% of total).

Northern-Southern Whitebelly Spinner Dolphin Differentiation.—

Table 5 indicates that three characters entered the discriminant function for separating northern and southern whitebelly spinner dolphins. The most important single character was Skull W.(at Zygomatic P.). The degree of separation of the two groups of whitebelly spinner dolphins is graphically depicted in Figure 11. It is clear from this figure that the "unknowns" from blocks 0405 and 0407 are appropriately considered as belonging to the northern group.

The classification functions (Table 5) correctly identified to group 86.4% of the 88 "known" specimens. A total of 30 (85.7%) of the 35 northern whitebelly specimens were appropriately allocated, as were 46 (86.8%) of the 53 southern whitebelly animals. Using the jackknifed approach, 84.1% of the 88 were identified correctly, including 29 (82.9%) of the 35 northern whitebelly and 45 (84.9%) of the 53 southern whitebelly spinner dolphins. Both procedures allocated the "unknowns" to the northern group.

Eastern, Northern Whitebelly, and Southern Whitebelly Spinners.—

The canonical variates developed to separate the spinner dolphins into these three groups included seven characters (Table 6), with the single most important character clearly being Postorbital W. (see F-value in Table 6). In Figure 12, specimens are plotted with respect to the canonical variables. The southern whitebelly spinners tend to be to the left and somewhat to the top of the diagram, while the northern whitebelly spinners are more centrally located and nearer the bottom. Most of the eastern spinner dolphins are to the right of plot. The "unknowns" are situated in the region of the northern whitebelly specimens.

In Table 7, we summarize the results of employing the three classification functions (Table 6) to allocate spinner dolphin specimens to one of the three groups. Overall, the regular procedure correctly identified 84.8% of the specimens, while the jackknifed approach resulted in 82.7% of the animals being classified in the correct group. As in previous analyses, the two "unknowns" were allocated to the northern whitebelly spinner group.

DISCUSSION

Perrin et al. (1979) reviewed and evaluated the taxonomic status of "southwestern" stocks (which they concluded were more appropriately designated as "southern") of spotted and spinner dolphins, and compared animals from the southern part of the range of these species with those

found in other parts of the eastern tropical Pacific. They concluded that the "southwestern" spinner dolphins are clearly modally different from the whitebelly spinners to the north.... This morphological difference between the animals north and south of the equator leads to the inference that some degree of genetic isolation exists, i.e., that the spinner dolphins south of the equator largely belong to a different breeding population than those to the north."

For the spotted dolphins, Perrin et al. (1979) found a very similar situation and concluded that "differences in morphology between the animals from below the equator and those to the north suggest some degree of isolation of the southern portion of the known distribution of the species...and a 'southern' population can be defined (based...on a near hiatus of records...)." They brought up the possibility that "the modal differences between the populations in one or both cases [species] are due to differential exploitation (perhaps affecting age and length at maturity)" and indicated that it "cannot be completely eliminated." However, this was considered to be very improbable, since external size differences between northern and southern animals are opposite in spotted and spinner dolphins. They judged that it is much more likely that the differences are genetically based.

We found similar trends but with a much larger data base (Schnell et al. 1982); there was extensive covariation between spotted and spinner dolphins, with variation in body size being negatively associated in the two species. For most skull measures, there was a positive association in geographic trends of the two species, but for some characters--like measurements of the temporal fossa--an inverse relationship was found. Certainly, both of the species showed differences between northern and southern areas. Our purpose in the present work was to further analyze, for both species, the degree of difference found in animals of the two areas. In addition, for the spinner dolphins, it also was instructive to assess these differences and how they relate to those found between eastern and whitebelly animals.

Northern-southern spotted dolphin differentiation.--Using cranial measures and a discriminant function, we were able to correctly identify over 87% of our specimens based on a jackknifed technique, an approach that "corrects" for the fact that one is evaluating the performance of an equation with specimens that were used to construct the function. Our ability to appropriately allocate specimens to group was not as great as in the analysis of inshore and offshore spotted dolphins, all specimens were identified correctly using a discriminant function based on cranial characteristics (Schnell et al. 1982, Douglas et al. 1984). However, this is not surprising; the inshore and offshore forms are highly distinctive and it is recognized that the northern-southern separation in spotted dolphins is not as great.

Nevertheless, marked differences do exist between those animals from the north and south, and a high proportion of animals can be identified as being from one area or the other, simply on the basis of cranial morphometric characteristics. This finding provides additional support--when taken along with the geographic trends and those of interspecific covariation summarized above and detailed in earlier

publications—for the recognition of the southern spotted dolphins as representing a largely separate population from those found to the north.

Northern-southern spinner dolphin differentiation.—The differences in cranial morphology of spinner dolphins in the south from those in the north are even more pronounced than those documented above for spotted dolphins. Over 94% were identifiable to geographic area using discriminant analysis. The degree of morphological separation suggests that the southern spinners are to some extent genetically partitioned from spinners to the north, since it would be highly improbable to find this degree of subdivision if there was frequent interchange of animals from the two geographic regions.

Whitebelly-eastern spinner dolphin differentiation.—As pointed out by Perrin (1975a, 1975b), the whitebelly and eastern spinners are clearly distinguishable on the basis of external characteristics. As an initial step, we were interested in determining whether or not the basic trends in sex differences found for spinner skulls from the eastern tropical Pacific were different, since a correction had been made in our geographic variation analysis to partition out the effect of sexual dimorphism—a correction based on samples from throughout the range and calculated without regard to external color characteristics of the specimens. Given the low number of characters showing significant interactions of color and sex—whether treating one 5° latitude-longitude block or the blocks where the two color forms overlap—there is no reason to use different corrections for sexual dimorphism in whitebelly and eastern spinners.

The extent of separation of whitebelly and eastern spinners based on cranial characters allowed for correct identification of 92% of the specimens. This was slightly less than that found for northern versus southern spinners, but still indicates substantive differences between the two color forms; much of the difference corresponds with the strong north-south geographic trends outlined in detail by Schnell et al. (1982). Not surprisingly, the proportion of animals that could be correctly allocated decreased when considering only specimens from the area of sympatry between the two color morphs; in this case, about 83% were correctly identified.

Northern-Southern Whitebelly Spinner Dolphin Differentiation.—The initial allocation of specimens to the whitebelly and eastern spinner groups, of course, is based on external color characteristics. Since eastern spinners do not occur in the southern part of the spinner dolphin range in the eastern tropical Pacific Ocean, we also wanted to assess the extent of northern-southern differentiation, considering only whitebelly specimens. Given that the geographic range of the whitebelly spinners in the northern area is considerably less than that for both color types, it would be expected that the degree of north-south differentiation and the ability to correctly allocate specimens would be somewhat less than for the analyses using all specimens. While this in fact was the case, it still was possible to identify correctly over 84% of the specimens using the jackknifed approach. This more limited analysis supports the idea that there are notable differences, at least on average, between northern and southern whitebelly spinners.

Eastern, Northern Whitebelly, and Southern Whitebelly Spinners.—As expected, our ability to correctly allocate specimens to one of three groups was reduced over that when only the two whitebelly groups were considered. However, the reduction was very slight, and it was possible to correctly assign over 82% of spinner specimens (using the jackknifed procedure) in terms of whether they were eastern, northern whitebelly, or southern whitebelly spinner dolphins.

On the basis of the several analyses completed to assess differentiation in spinner dolphins, it is clear that there are cranial morphometric differences between whitebelly and eastern spinner dolphins, but an even stronger difference between animals from northern and southern areas. The morphological data suggest that spinner dolphin populations are subdivided in the eastern tropical Pacific Ocean in such a way that gene flow is restricted, at least in portions of the species' range. Clearly, the spinner dolphins of the eastern tropical Pacific are not appropriately treated for management or other purposes as a panmictic unit, but the effects of isolation by distance, as well as partial geographic isolation, must be taken into account. The morphological studies of Schnell et al. (1982) gave strong evidence of geographic subdivision, and the follow-up analyses reported here further support such a conclusion.

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Table 1.--Statistics for stepwise discriminant analysis of northern and southern offshore spotted dolphins. Specimens from block 0501 were not included when calculating the functions.

Character	F-value to enter	Order of entry	Discriminant function coefficients		Classification function ^a	
			Unstandardized	Standardized	North	South
4 W. Rostrum (at Base)	12.94	5	-0.0873	-1.0169	1.291	1.504
9 Preorbital W.	87.32	1	-0.0548	-0.6376	2.002	2.135
11 Skull W.(at Zygomatic P.)	7.30	8	-0.1008	-1.1736	1.721	1.967
13 Ht. Braincase	7.59	9	0.0631	0.7345	5.330	5.176
18 W. Rt. Premax.(md.Nares)	23.74	4	-0.1723	-2.0065	4.835	5.256
19 L. Temporal Fossa	6.26	10	0.0510	0.5940	-0.729	-0.853
20 W. Temporal Fossa	88.47	2	0.1054	1.2270	1.833	1.575
21 Orbital L.	9.58	6	-0.1004	-1.1693	8.806	9.051
26 L. Rt. Tympanic Cavity	8.38	7	0.0884	1.0295	1.192	0.976
33 L. Low. Tooth Row	25.48	3	0.0565	0.6584	0.756	0.618
Constant				13.2110	-1036.184	-1060.734

^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as northern or southern depending on which has the higher value for its classification function.

Table 2.--Statistics for stepwise discriminant analysis of northern and southern spinner dolphins.

Character	F-value to enter	Order of entry	Discriminant function coefficients		Classification function ^a	
			Unstandardized	Standardized	North	South
6 W. Rostrum (at 1/2 L.)	9.02	4	-0.1341	-1.8043	1.433	1.852
8 W. Rostrum (at 3/4 L.)	22.63	2	0.2681	3.6079	-2.914	-3.750
10 Postorbital W.	213.58	1	-0.1273	-1.7131	2.856	3.254
12 Skull W.(at Parietals)	5.52	6	0.0900	1.2110	3.036	2.755
13 Ht. Braincase	7.48	7	-0.0924	-1.2439	3.219	3.507
14 L. Braincase	5.71	5	-0.0770	-1.0356	5.292	5.532
24 W. Internal Nares	14.02	3	-0.1714	-2.3061	-0.907	-0.372
Constant			28.5260		-784.633	-875.813

^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as northern or southern depending on which has the higher value for its classification function.

Table 3.--Statistics for stepwise discriminant analysis of the 193 eastern and whitebelly spinner dolphins.

Character	F-value to enter	Order of entry	Discriminant function coefficients		Classification function ^a	
			Unstandardized	Standardized	Eastern	Whitebelly
10 Postorbital W.	248.04	1	-0.1986	-2.8425	3.725	4.268
12 Skull W.(at Parietals)	6.42	4	-0.0984	1.4081	3.644	3.375
13 Ht. Braincase	10.98	5	-0.1096	-1.5681	3.172	3.472
20 W. Temporal Fossa	17.13	2	-0.1584	-2.2671	1.314	1.747
26 L. Lf. Tympanic Cavity	9.29	3	0.1181	1.6904	1.687	1.364
Constant				27.6763	-706.034	-781.927

^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as eastern or whitebelly depending on which has the higher value for its classification function.

Table 4.--Statistics for stepwise discriminant analysis of the 59 sympatric eastern and whitebelly spinner dolphins.

Character	F-value to enter	Order of entry	Discriminant function coefficients		Classification function ^a	
			Unstandardized	Standardized	Eastern	Whitebelly
5 W. Rostrum(at 1/4 L.)	7.36	4	-0.2461	-3.5893	2.053	2.565
7 W. Premax.(at 1/2 L.)	4.47	3	0.5107	7.4486	-5.815	-6.878
10 Postorbital W.	27.62	1	-0.2420	-3.5296	8.288	8.792
26 L. Lf. Tympanic Cavity	8.63	2	0.2628	3.8336	-0.288	-0.835
Constant			27.0990		-602.007	-658.150

^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as eastern or whitebelly depending on which has the higher value for its classification function.

Table 5.--Statistics for stepwise discriminant analysis of 90 whitebelly spinner dolphins.

Character	F-value to enter	Order of entry	Discriminant function coefficients		Classification function ^a	
			Unstandardized	Standardized	Northern	Southern
8 W. Rostrum(at 3/4 L.)	20.55	2	0.2602	1.3538	-1.006	-1.591
11 Skull W.(at Zygomatic P.)	52.11	1	-0.2502	-3.6128	9.909	10.472
35 Tooth W.	10.29	3	-2.1093	-30.4622	88.676	93.418
Constant				36.6906	-864.152	-946.110

^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as northern or southern depending on which has the higher value for its classification function.

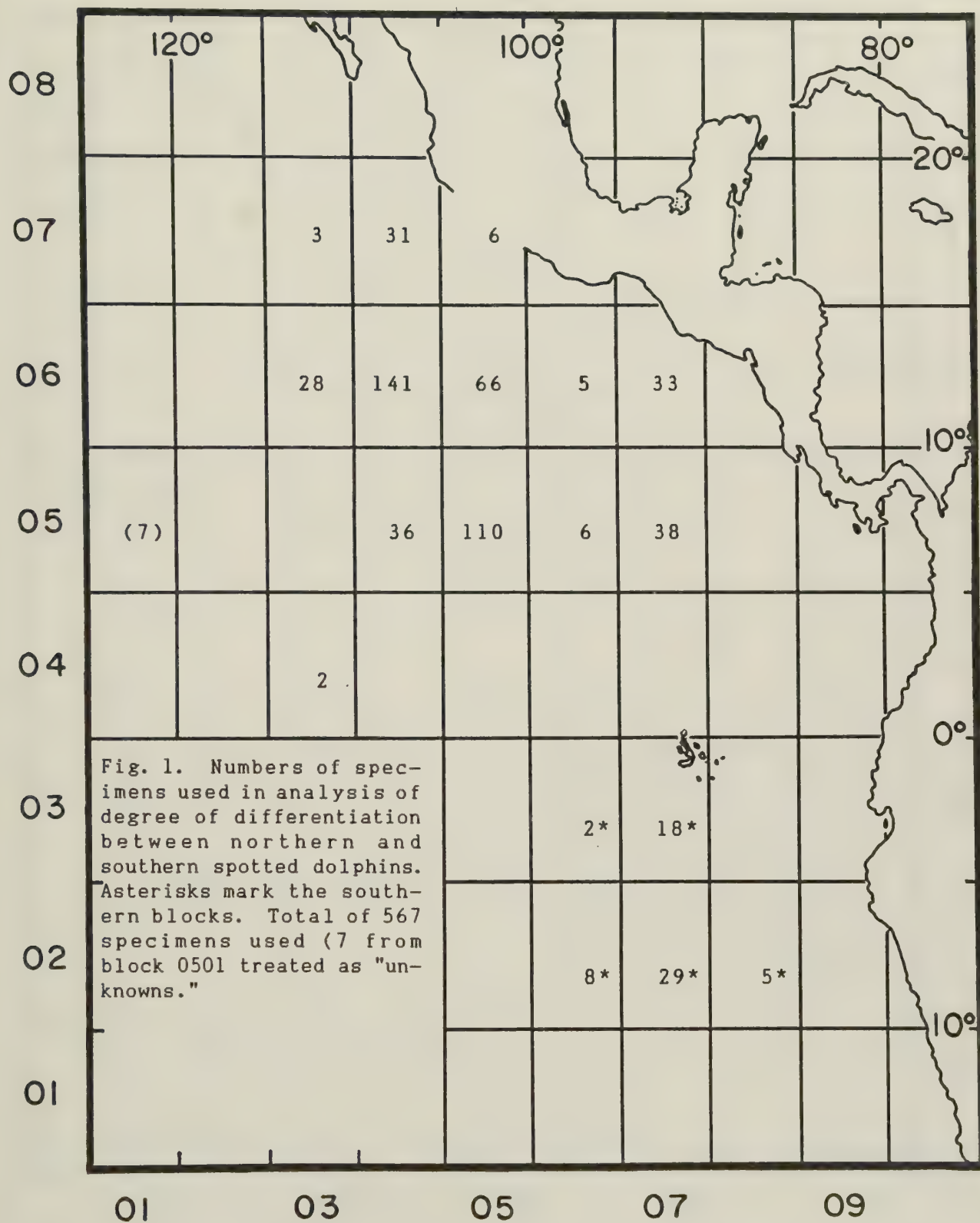
Table 6.--Statistics for canonical variates analysis of eastern spinner dolphins and northern and southern whitebelly spinner dolphins.

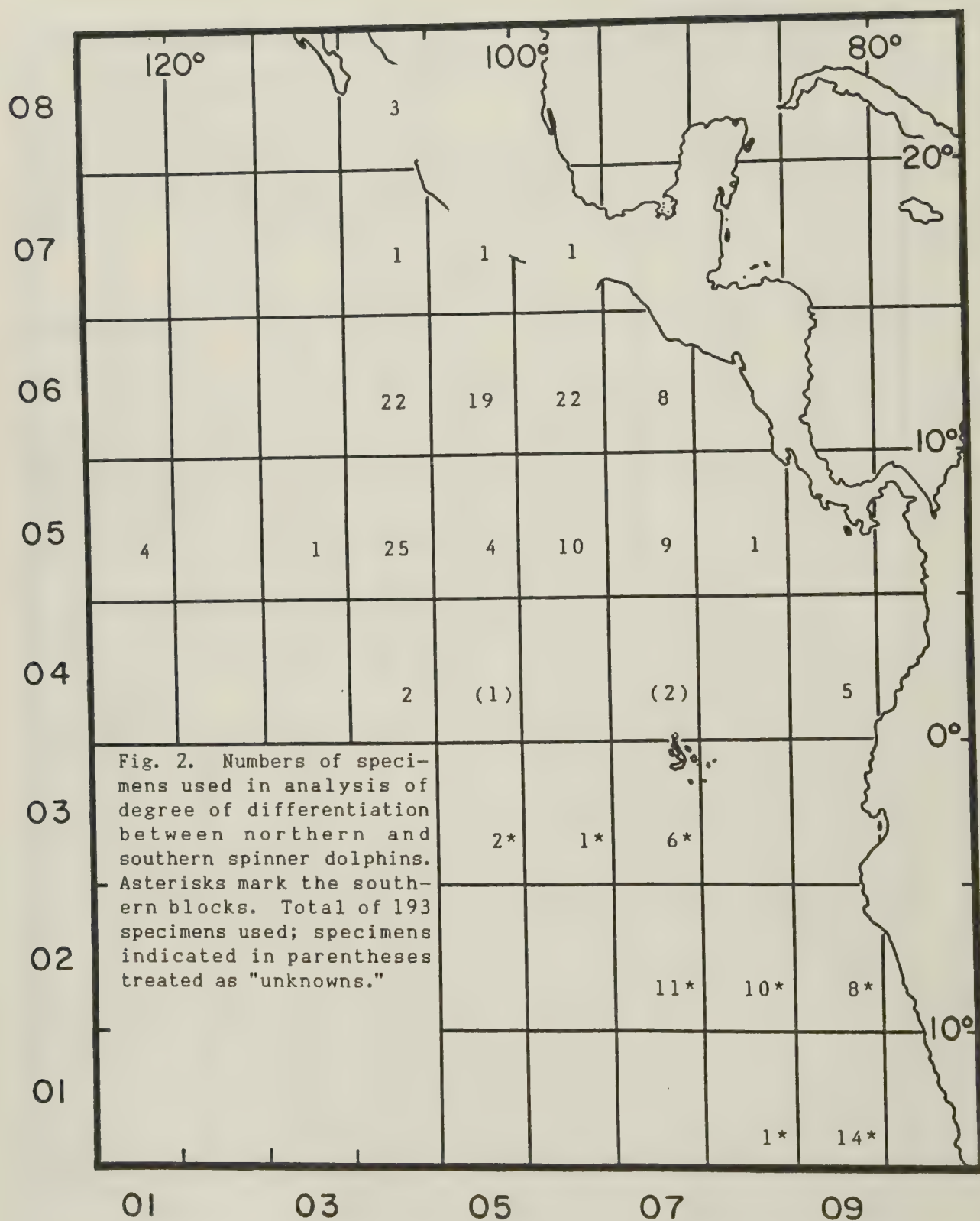
Character	F-value to enter	Order of entry	Canonical variable coefficients				Classification function ^a		
			Unstandardized		Standardized		Eastern	Northern	Southern
			1	2	1	2			
8 W. Rostrum (at 3/4 L.)	11.60	2	0.105	-0.312	1.374	-3.333	-1.855	-1.761	-2.316
10 Postorbital W.	183.40	1	-0.206	-0.016	-2.700	-0.167	5.813	6.238	6.638
12 Skull W.(at Parietals)	4.57	6	0.112	-0.015	1.471	-0.162	2.684	2.476	2.232
13 Ht. Braincase	7.58	7	-0.123	0.003	-1.609	0.034	4.446	4.687	4.939
20 W. Temporal Fossa	8.97	3	-0.120	-0.189	-1.583	-2.018	1.657	2.080	2.117
24 W. Internal Nares	7.04	4	-0.145	0.183	-1.897	1.961	0.354	0.464	0.959
24 L. Lf. Tympanic Cavity	5.30	5	-0.059	0.228	0.778	2.440	2.109	1.770	1.900
Constant			32.264	2.641	32.264	2.641	-848.218	-914.354	-979.611

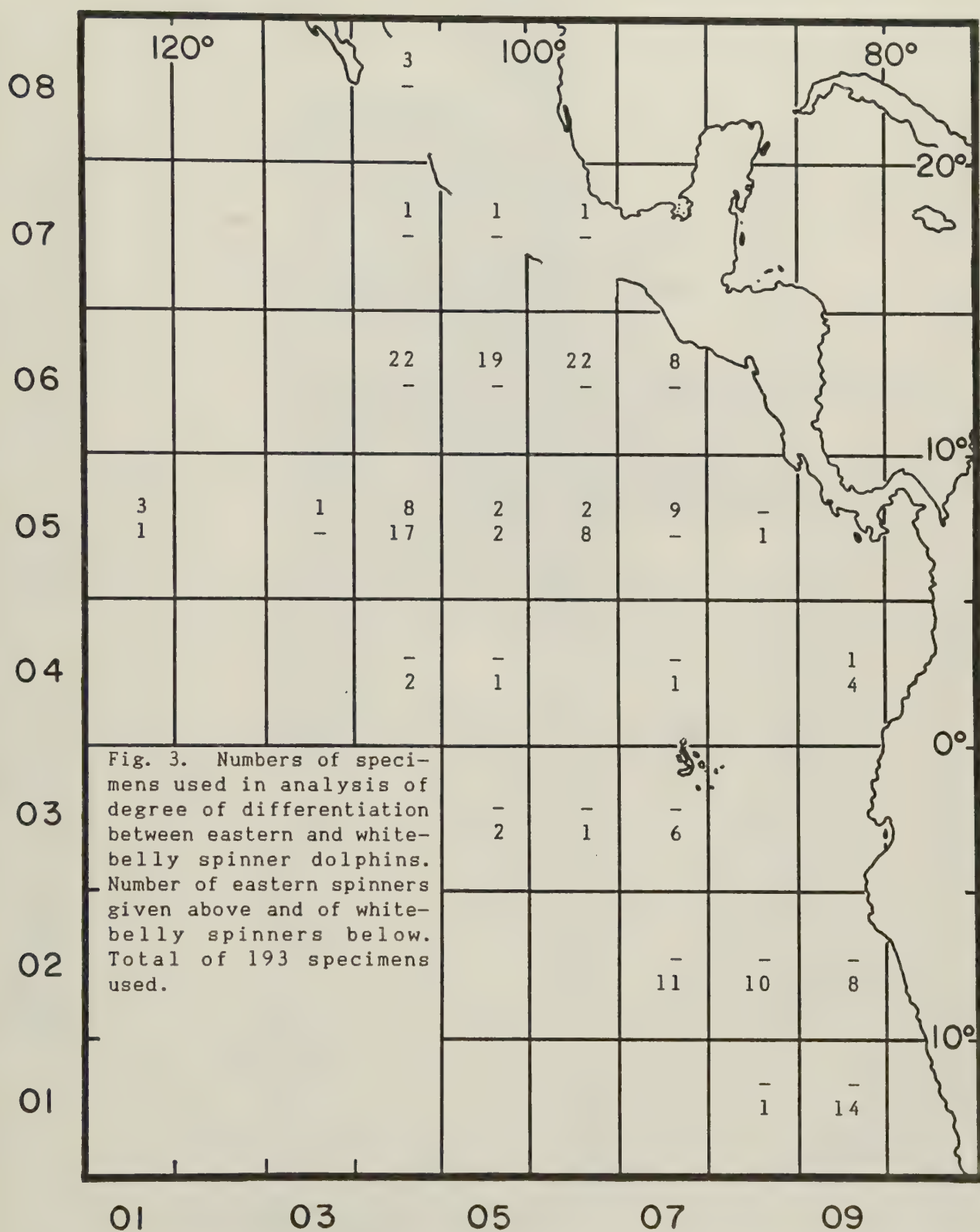
^aUsed with original measurements (corrected to zwitter values). Add products of zwitter values and function values to constant; classify as eastern, northern whitebelly, or southern whitebelly spinner dolphin, depending on which has the highest value for its classification function.

Table 7.--Number of specimens identified as eastern, northern whitebelly, and southern whitebelly spinner dolphins by classification functions using the regular and pseudo-jackknifed procedures.

Original group	Allocated to			Percent correct
	Eastern	Whitebelly		
		Northern	Southern	
<u>Regular procedure</u>				
Eastern	89	14	0	86.4
N. whitebelly	2	29	4	82.9
S. whitebelly	0	9	44	83.0
Unknown	0	2	0	--
Total	91	54	48	84.8
<u>Pseudo-jackknifed procedure</u>				
Eastern	88	14	1	85.4
N. whitebelly	5	26	4	73.4
S. whitebelly	0	9	44	83.0
Unknown	0	2	0	--
Total	93	51	49	82.7







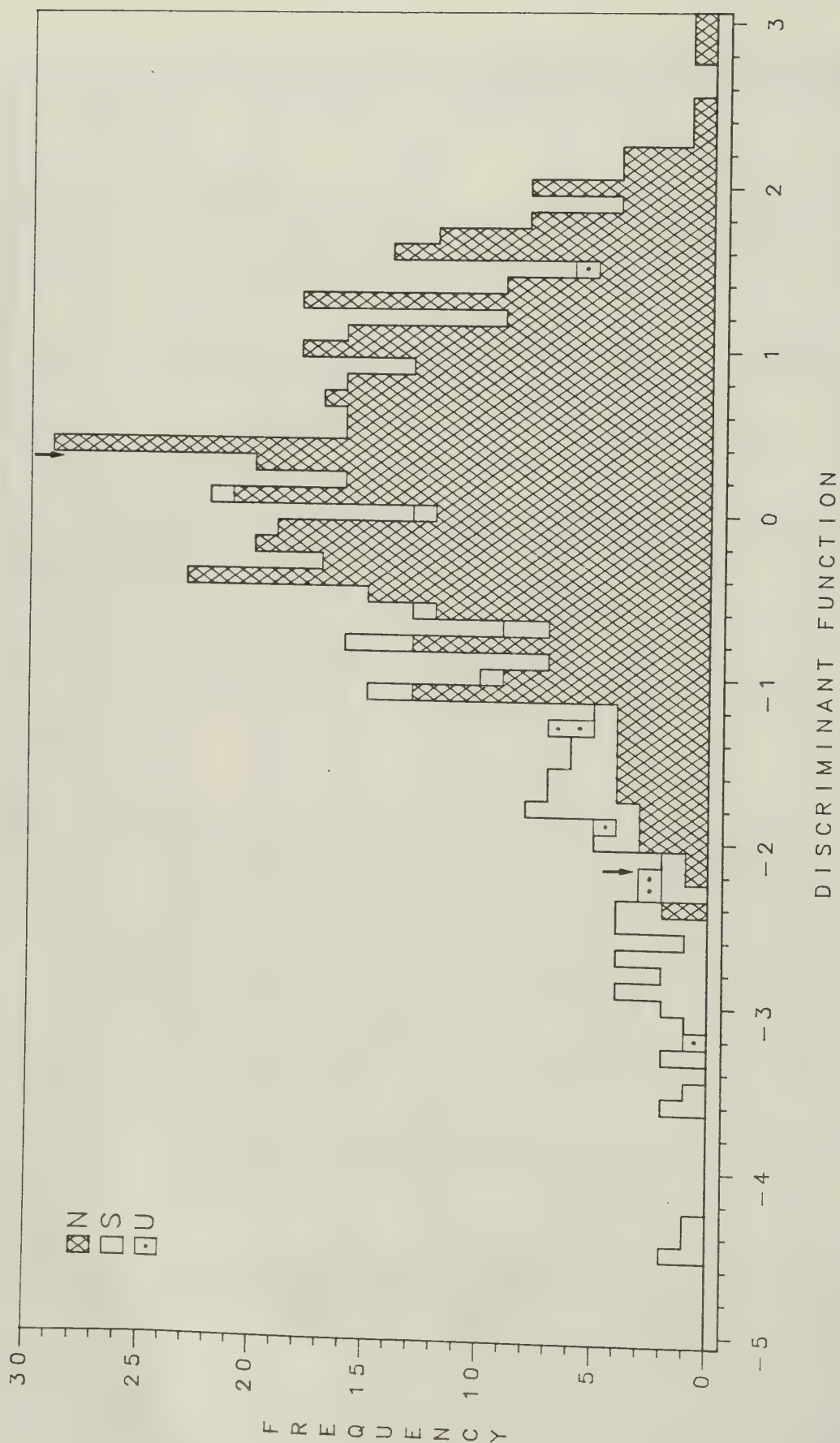


Fig. 4. Projections of spotted dolphins onto the discriminant function axis for separating northern and southern specimens. Arrows indicate mean values for each group. Placement of specimens from block 0501-- considered as "unknowns"--is indicated.

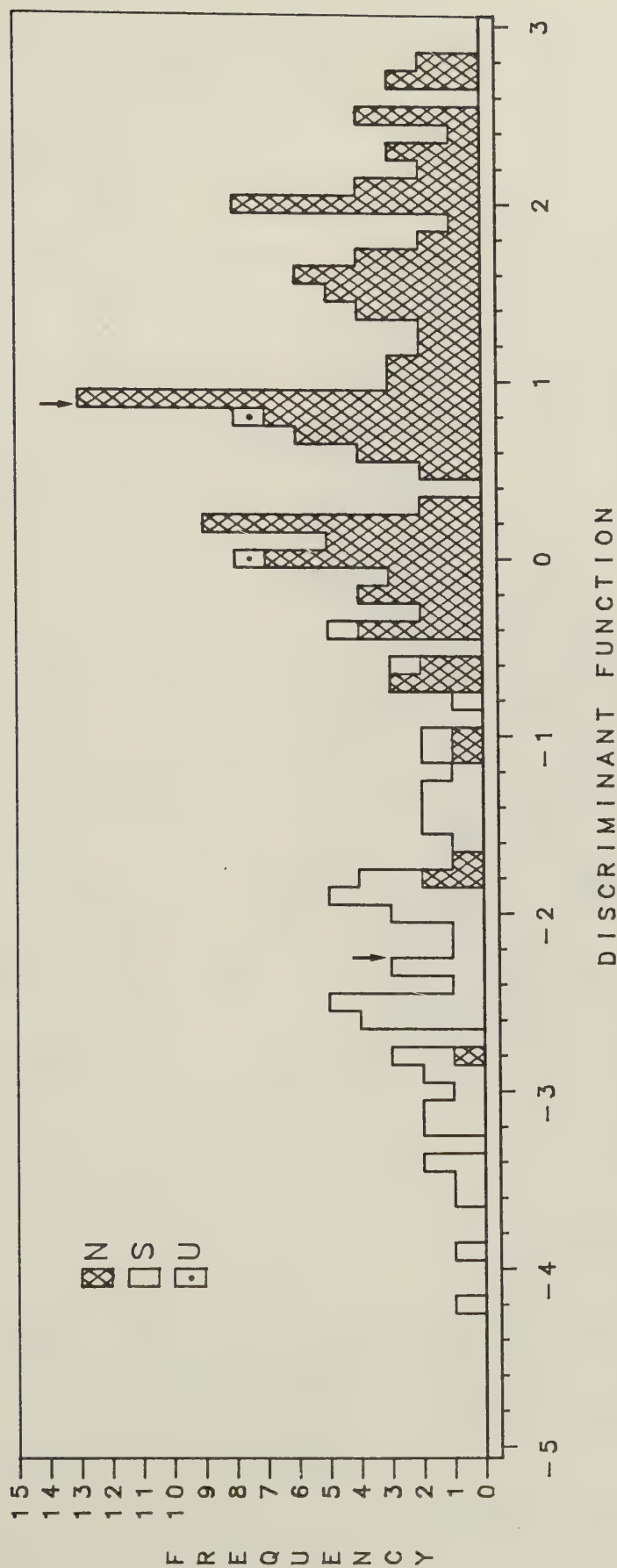


Fig. 5. Projections of 193 spinner dolphins onto the discriminant function axis for separating northern and southern specimens. Arrows indicate mean values for each group. The single specimens from blocks 0405 and 0407 were treated as "unknowns."

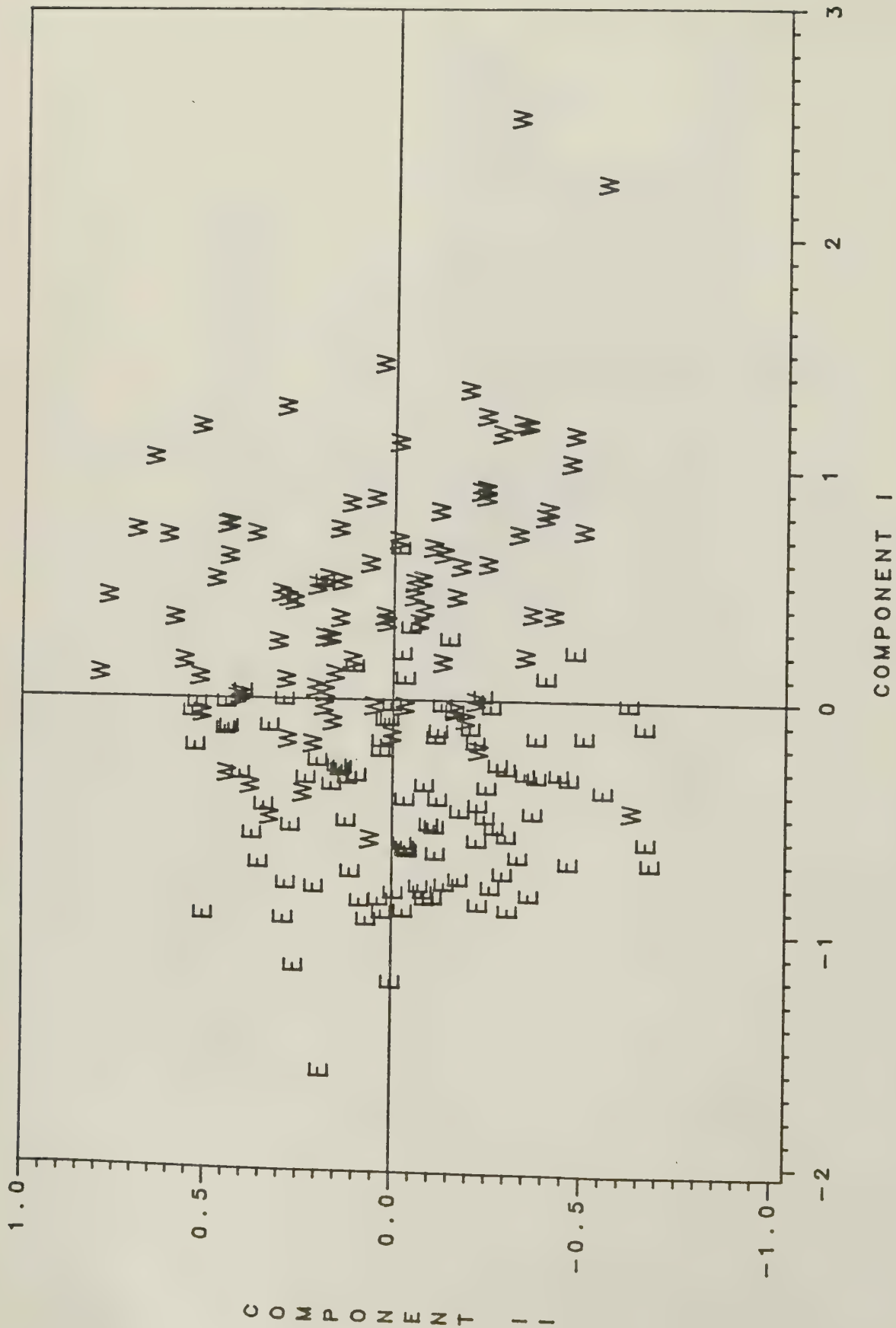


Fig. 6. The 193 eastern and whitebelly spinner dolphins plotted with respect to the first two principal components based on 36 cranial characters.

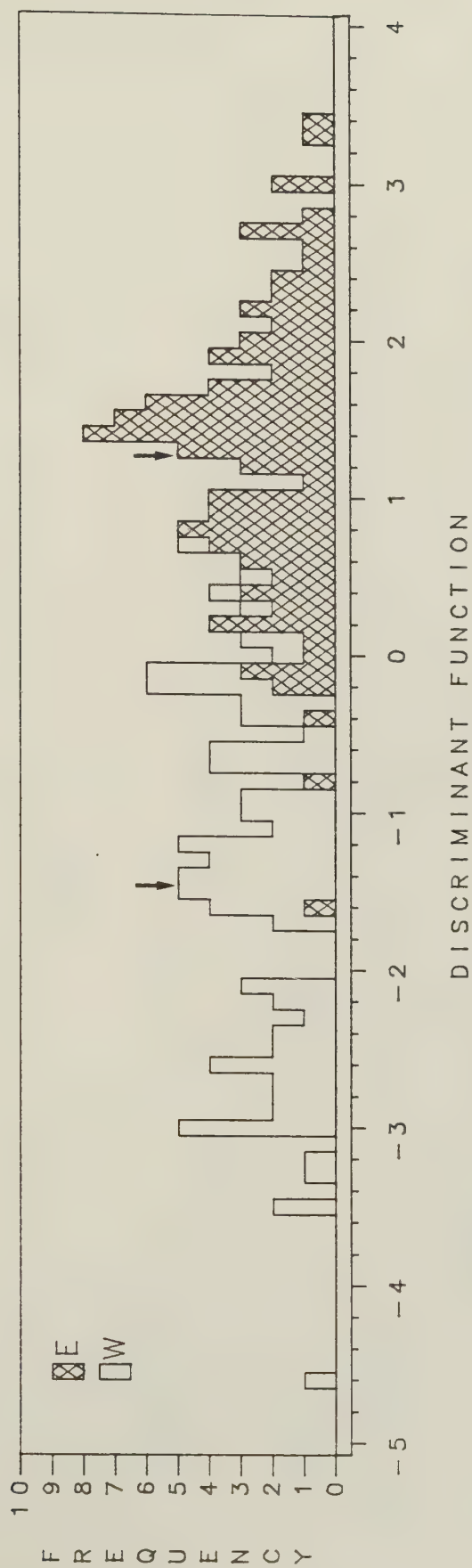


Fig. 7. Projections of 193 spinner dolphins onto the discriminant function axis for separating eastern and whitebelly specimens. Arrows indicate mean values for each group.

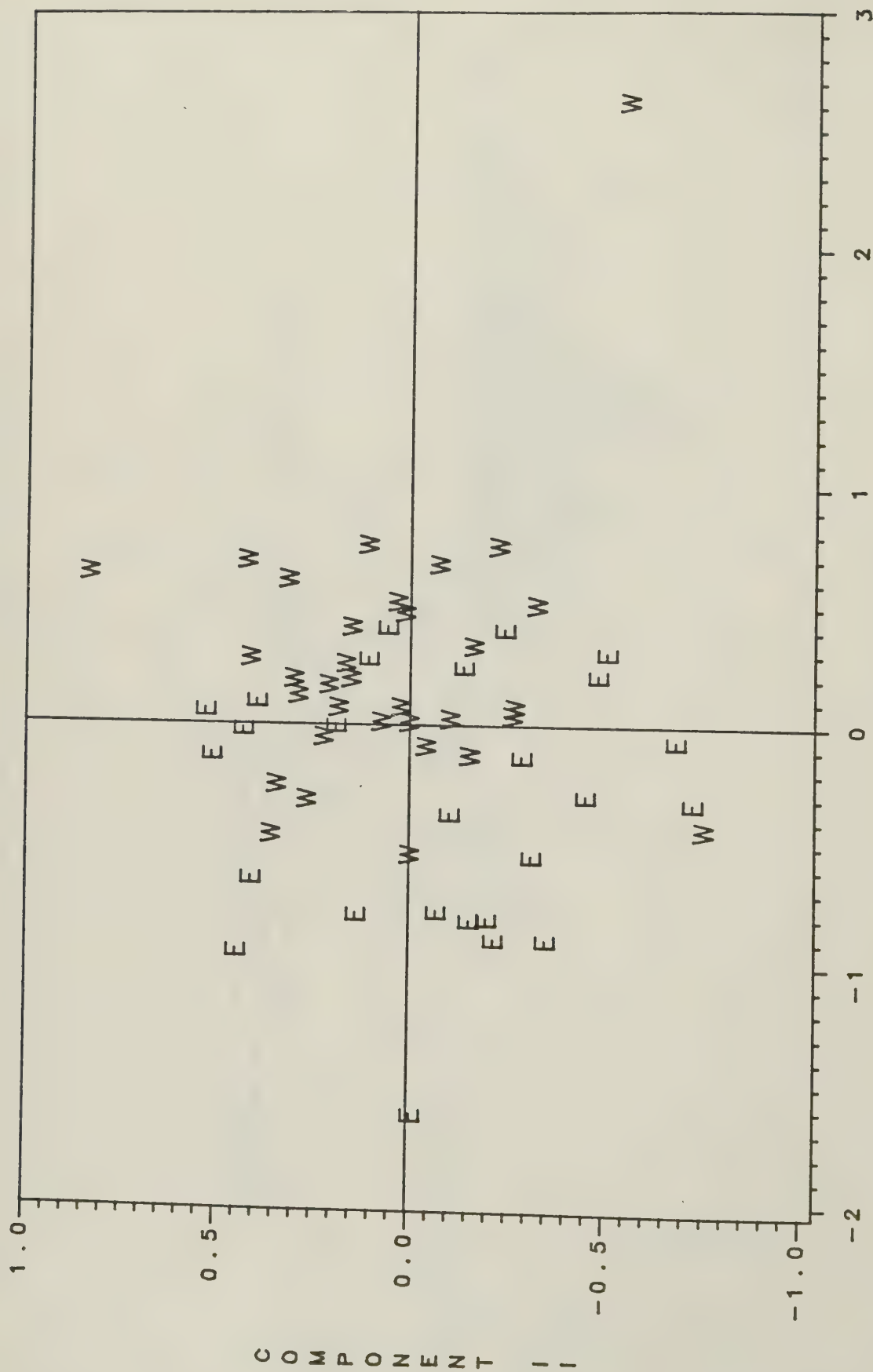


Fig. 8. The 59 eastern and whitebelly spinner dolphins from area of sympatry plotted with respect to the first two principal components based on 36 cranial characters (and these 59 specimens only).



Fig. 9. Distance phenogram showing associations of 59 spinner dolphin specimens from area of sympatry of eastern and whitebelly forms based on 36 cranial characters. Individual specimens are identified in labels by E (eastern) or W (whitebelly), followed by the block number (e.g., 501 = 0501) and a specimen number within that block. The cophenetic correlation is 0.86.

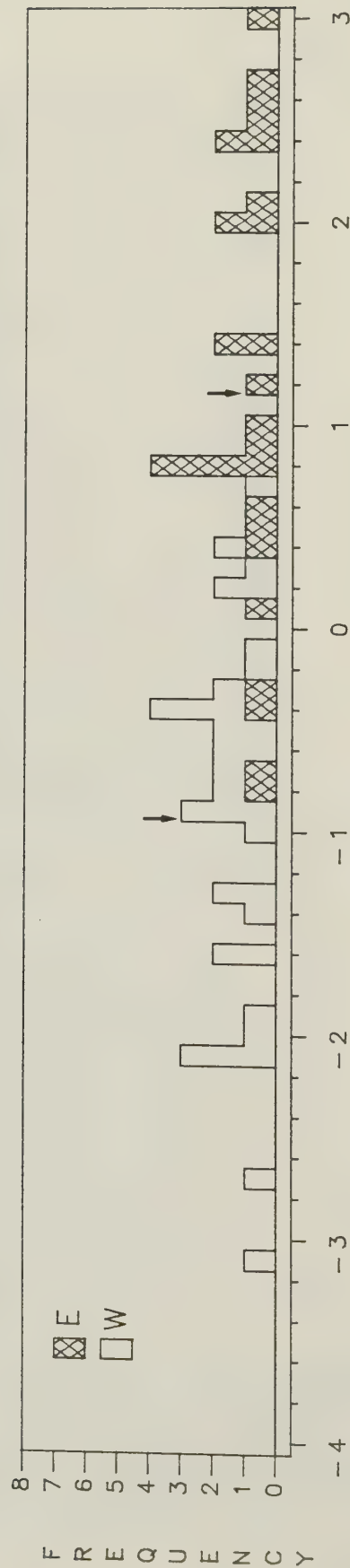


Fig. 10. Projections of 59 spinner dolphins from area of sympatry onto the discriminant function axis for separating eastern and whitebelly specimens (and based only on those specimens in area of sympatry). Arrows indicate mean values for each group.

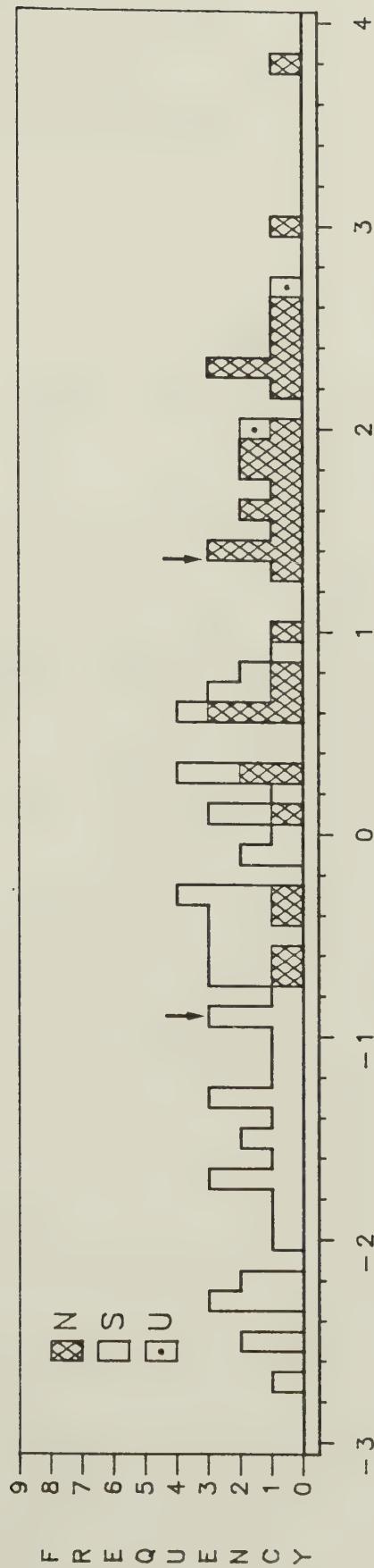
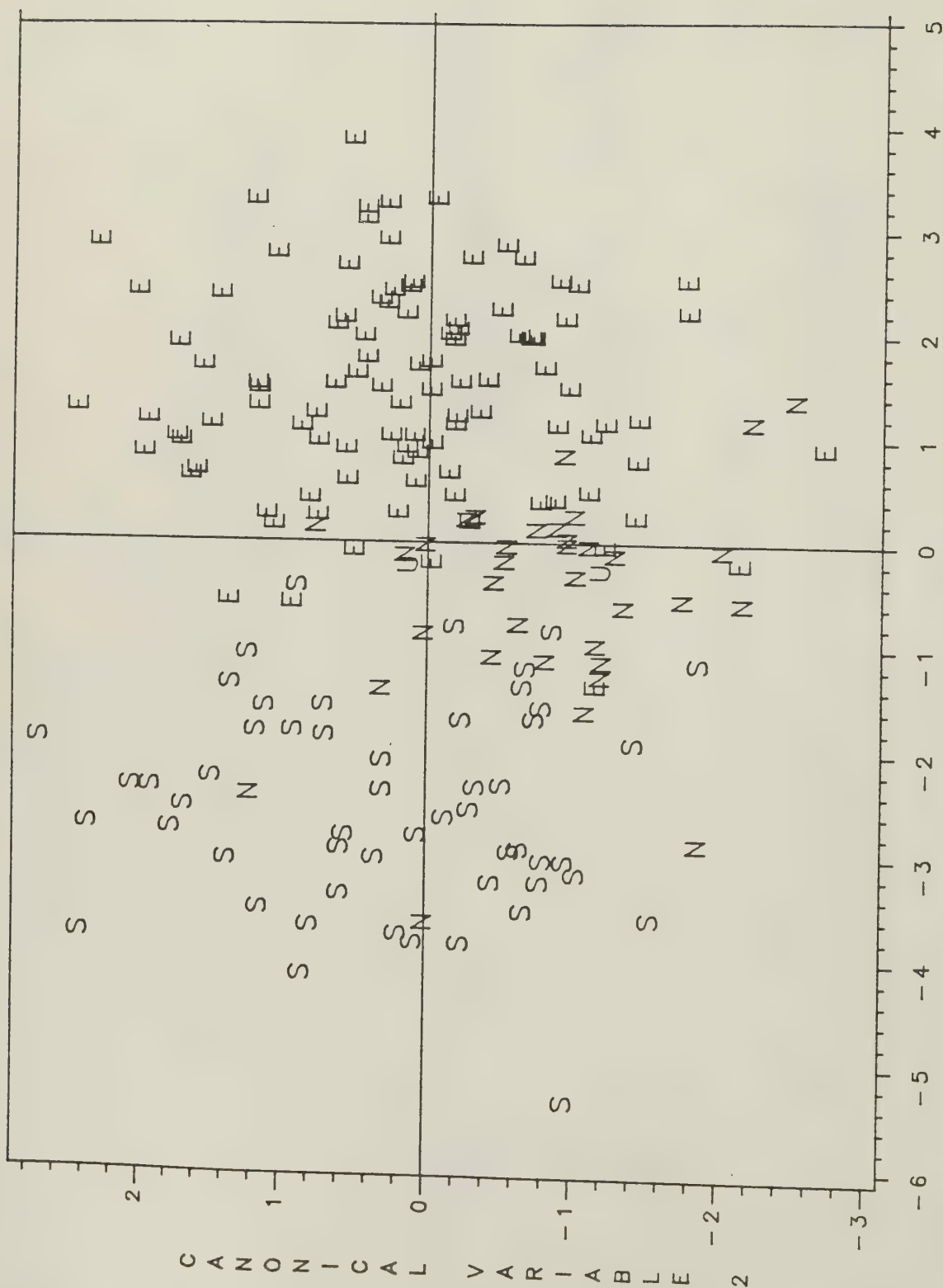


Fig. 11. Projections of 90 whitebelly spinner dolphins onto the discriminant function axis for separating northern and southern whitebelly specimens. Arrows indicate mean values for each group. The single specimens from blocks 0405 and 0407 were treated as "unknowns."



CANONICAL VARIABLE 1

Fig. 12. Projections of 193 spinner dolphins onto the two canonical variables based on three groups: 103 eastern (E); 35 northern whitebelly (N); and 53 southern whitebelly (S). The single specimens from blocks 0405 and 0407 were treated as "unknowns" (U).

